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Structural changes within trophic levels are constrained by within-family assembly rules at lower trophic levels

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Abstract

Historical contingency broadly refers to the proposition that even random historical events can constrain the ecological and evolutionary pathways of organisms and that of entire communities. Focusing on communities, these pathways can be reflected into specific structural changes within and across trophic levels—how species interact with and affect each other—which has important consequences for species coexistence. Using the registry of the last 2000 years of plant introductions and their novel herbivores encountered in Central Europe, we find that the order of arrival of closely-related (but not of distantly-related) plant species constrained the structural changes within the trophic level formed by herbivore species across the observation period. Because it is difficult for field and lab experiments to be conducted over hundreds of years to record and replay the assembly history of a community, our study provides an alternative to understand how structural changes have occurred across extensive periods of time.

Introduction

In 1989, Stephen J. Gould posed the thought experiment of whether evolutionary history would take a very different route than the one we know today if we could rewind the tape of life and replay it again (Gould, 1989). While historical events are difficult to reconstruct and replay over long periods of time, it has been shown that it may be possible to investigate the assembly rules shaping the biodiversity that we observe in nature (Thompson, 1917; Fox, 1987; Alberch, 1989). Historical contingency broadly refers to the proposition that even random historical events (such as abiotic and biotic events) can constrain the ecological and evolutionary pathways of organisms and that of entire ecological communities (Fukami, 2015). In an ecological context, these pathways can be reflected into specific structural changes within and across trophic levels, which are defined by how species interact with and affect each other (Odum, 1969; Dormann et al., 2017; Godoy et al., 2018). This structure, which is summarized by the interaction matrix, has key implications for species coexistence (Case, 2000; Saavedra et al., 2017*b*), and is highly dependent on the order and timing of species arrivals to the community (Diamond, 1975; Chase, 2003; Morin, 2011). While assembly processes and their effects are typically investigated within a focal trophic level, numerous studies have shown that these effects can also impact the composition of species across different trophic levels (Drake, 1991; Olito and Fukami, 2009; Price and Morin, 2004; Fukami, 2015; Gomes et al., 2017). Yet, it remains unclear which are the main historical factors explaining the structural changes that we observe across trophic levels over time.

To shed new light onto the questions above, we study the order of arrival within the trophic level formed by plant species and its effect on the structure of the herbivore trophic level feeding on these plants. We study the structure of the herbivore trophic level by looking at how the competition matrix among herbivores (formed by shared plants) modulates the range of environmental conditions compatible with the persistence of the herbivore community—a measure that is typically called the structural stability of community persistence (Saavedra et al., 2017*a*,*b*). Because it is difficult for field and lab experiments to be conducted over extensive periods of time in order to record the assembly history of a community (Fukami and Morin, 2003; Chase, 2010; Leopold et al., 2017), we investigate historical events using the registry of the last 2000 years of plant

introductions to Central Europe and the existing native herbivore communities in that region. These data allow us to answer the two following questions: Are there non-trivial structural changes within the herbivore trophic level formed by herbivore species competing for (sharing) plant-hosts? How does the order of plant arrivals within and across families constrain structural changes within the herbivore trophic level?

Methods

Observational data

We based our analysis on a plant-herbivore interaction matrix from the German State of Baden-Württemberg (35,751 km^2) in Central Europe (Altermatt and Pearse, 2011; Pearse and Altermatt, 2013*a*,*b*, 2015). In a collaborative long-term effort (Ebert, 1991-2005), herbivory observations of > 2.342 million larval individuals of 759 Macrolepidopteran (i.e., butterflies and moths) species were recorded feeding on a total of 684 vascular plant species. All observations refer to interactions which have been observed under natural conditions in Baden-Württemberg since the beginning of the 20th century (Altermatt and Pearse, 2011), possibly making it one of the most complete large plant-insect interaction datasets (see Pearse and Altermatt (2015) for tests of completeness and robustness).

In our data, all Macrolepidopterans and 501 vascular plants are native to Baden-Württemberg. Additionally, 183 vascular species are non-native plants, which can be further divided into 22 archaeophytes (naturalized non-native plants that arrived prior to 1492), 63 neophytes (naturalized non-native plants that arrived after 1492), and 98 ornamentals (non-native plants that do not have self-sustained populations in Baden-Württemberg). Note that novel plant-insect interactions have been observed between native lepidopterans and non-native plants (Pearse and Altermatt, 2013*b*).

To establish the most probable introduction year, we also assembled estimates of the plant-arrival times in Baden-Württemberg (or, if not available, in Central Europe) based on archaeobotanical and historical records (Sebald et al., 1993-1998; Jacomet and Brombacher, 2009; Klotz et al., 2002). For each plant, we cross-referenced arrival dates across these sources, additional archaeobotanical records, historical texts such as regional gardening journals, and herbarium and botanic garden records in order establish the

most probable introduction year. The arrival times for plants arriving within the last two centuries were precise to 1 to 10 years. In turn, the arrival times were precise to 50 to 100 years for plants arriving before the last two centuries and after the middle ages. Similarly, the arrival times for plants arriving before the middle-ages were precise to 100 years. Older records may be conservative estimates, particularly as they are generally based on the oldest remains of these plants to be found.

These aggregated data were stored in a meta matrix (a binary matrix that we called $\boldsymbol{\beta}$), where each row i and column j corresponds to an observed plant and an observed herbivore species, respectively. Each binary element of this meta matrix represents the presence ($\beta_{ij} = 1$) or absence ($\beta_{ij} = 0$) of an observed plant–herbivore interaction between two species at any point across our observational period. We assumed that there is an interaction between two species as long as there is one record of it in our data. For arrival times, the data were stored as a vector, where each row corresponds to an observed plant species and its value corresponds to the plant's estimated arrival time. Then, for each arrival time t, we formed time-dependent matrices $\boldsymbol{\beta_t}$ by extracting subsets of the meta matrix, where each plant and herbivore species has an arrival time older or equal than t. Note that herbivore species will be part of a time-dependent matrix as long as any of its host-plants is also present (Fig. S1 illustrates how the number of herbivore species changes across time). These time-dependent matrices assume that there is no evolution in or rewiring of interaction preferences between plants and herbivores, that all lepidopterans can be present at any point in time throughout the study area, that depending on the presence and absence of species all of the possible interactions are always realized at a specific time, and species abundances do not affect the realization of interactions. While these are strong assumptions (Brändle et al., 2008; Faillace and Morin, 2016), without empirical information any other simulated process would add *ad hoc* free parameters to our study.

Inferring the competition matrix within the herbivore trophic level

We used the time-dependent matrices $\boldsymbol{\beta_t}$ to infer the time-dependent competition matrices within the herbivore trophic level (formed by herbivore species competing for

host-plants) (Saavedra et al., 2014, 2017a). Each time-dependent competition matrix (that we called $\boldsymbol{A_t}$) was inferred by the normalized monopartite projection of the binary matrix $\boldsymbol{\beta_t}$ (Cenci et al., 2018). Specifically, the monopartite projection corresponds to $\boldsymbol{M_t} = \boldsymbol{\beta_t}^T \boldsymbol{\beta_t}$. The off-diagonal entries of the monopartite projection correspond to the number of host-plants shared between two herbivores. Thus, the resource overlap between two herbivores i and j is proportional to the matrix element M_{ij} (MacArthur and Levins, 1967; Logofet, 1993). Normalizing the entries of the matrix $\boldsymbol{M_t}$ by the sum of their column (i.e., $A_{ij} = \frac{M_{ij}}{\sum_i M_{ij}}$), we have a time-dependent competition matrix $\boldsymbol{A}_t$, whose elements can be interpreted as the effect of herbivore species j on species i. That is, if the proportion of shared host-plants between herbivore species i and j is high relative to the total number of host-plants shared between species i and the rest of the species, the direct effect of species j on species i is high. However, if the two herbivore species do not share any host-plants, the direct effect is zero. Note that the effect of species j on i is not necessarily the same as the effect of species i on j. While it has been shown that the persistence of herbivore species depends on many factors, such as: resource availability, the presence of host species, natural enemies, and environmental variations, among others (Hairston et al., 1960; Gripenberg et al., 2007; Tack et al., 2009); it has been demonstrated that plant-mediated competition matrices provide explanatory power to the likelihood of herbivore persistence (Saavedra et al., 2017a; Cenci et al., 2018). Yet, we have not empirically demonstrated that competition occurs in this system, but we are instead assuming that it is an important, but undemonstrated, process in our analysis.

Estimating structural changes within the herbivore trophic level

As we mentioned before, the competition matrix within the herbivore trophic level is time dependent. That is, from the first to the last observed plant arrival, each time t a new plant arrives a new matrix $\boldsymbol{A_t}$ is formed. Thus, to investigate structural changes of $\boldsymbol{A_t}$ across time, we used a comparable measure of structural stability of community persistence. Formally, structural stability corresponds to the extent to which a system can tolerate modifications to its dynamics without changing its qualitative behavior (Thom, 1972). We measured the structural stability of community persistence by the extent to which each competition matrix $\boldsymbol{A_t}$ modulates the range of parameter values (environmental conditions) compatible with the persistence of all competing herbivores in

the community (Saavedra et al., 2017*b*).

To model the competition dynamics among herbivore species, we used a classic Lotka-Volterra (LV) competition model (MacArthur and Levins, 1967; Case, 2000). Mathematically, the LV dynamics of S competing species can be written as

$$\frac{dN_i}{dt} = N_i(r_i - \sum_{j=1}^{S} a_{ij}N_j),$$

where N_i corresponds to the abundance (or biomass) of species i, r_i is the intrinsic growth rate of species i, and a_{ij} are the elements of the competition matrix $\boldsymbol{A_t}$.

In this competition system, the structural stability of community persistence can be measured by the set of vectors $\boldsymbol{r} = [r_1, r_2, \ldots, r_s]^T$ that guarantees positive species abundances at equilibrium $N_i^* > 0$ as a function of $\boldsymbol{A_t}$ (Saavedra et al., 2014; Rohr et al., 2016). This parameter space is called the feasibility domain $D_F(\boldsymbol{A_t})$. The size of this domain can be computed by comparing it against the full parameter space of intrinsic growth rates. Because this domain is compressed of vectors, we are only interested in their direction (not in their magnitude) and the full parameter space can be normalized to a unit ball $\mathbb{B}^S$ made up of vectors with unit magnitude (expressed in terms of a norm). Therefore, the size of the feasibility domain can be calculated by the ratio of the following volumes (Ribando, 2006; Saavedra et al., 2016*b*):

$$\omega(\boldsymbol{A_t}) = (\frac{2\,\mathsf{vol}(D_F(\boldsymbol{A_t}) \cap \mathbb{B}^S \cap \mathbb{R}_+^S)}{\mathsf{vol}(\mathbb{B}^S \cap \mathbb{R}_+^S)})^{1/(S-1)},$$

where $\mathbb{B}^S \cap \mathbb{R}_+^S$ represents the normalized S-dimensional parameter space constrained to positive elements in the vectors (i.e., we assumed that species can only take positive intrinsic growth rates (Saavedra et al., 2017*b*)). This ratio can be computed by the cumulative distribution function of a multivariate normal distribution integrated over the positive abundance space (recall that $\boldsymbol{r} = \boldsymbol{A_t N^*} > 0$) and can be efficiently calculated even for relatively large communities (Ribando, 2006; Saavedra et al., 2016*b*). The larger $\omega(\boldsymbol{A_t})$, the larger the fraction of vectors of intrinsic growth rates compatible with the persistence of species at the herbivore trophic level. Thus, $\omega(\boldsymbol{A_t}) \in [0, 1]$ can be used as a comparable quantitative measure of structural stability of community persistence, and can be interpreted as the probability that a randomly chosen species i within the

herbivore trophic level characterized by the time-dependent competition matrix $\boldsymbol{A_t}$ can tolerate random environmental changes. Note that our measure of structural stability is not restricted to LV dynamics as long as the dynamics are topologically equivalent (Cenci and Saavedra, 2018).

Therefore, to investigate structural changes within the herbivore trophic level, we tracked how $\omega(\boldsymbol{A_t})$ changes over time by calculating the Pearson correlation between the vectors of structural stability and time, i.e., $r(t,\omega(\boldsymbol{A_t}))$. We investigated the robustness of the observed correlation to sampling error by systematically removing a fraction of randomly chosen plants and repeating the analysis above (Legendre and Legendre, 2012). Additionally, we performed a split sample test and calculated the corresponding piecewise correlations to evaluate potential nonlinear effects of different observational periods in the assembly order of plants on structural changes within the herbivore trophic level (Legendre and Legendre, 2012).

Validating structural stability as a measure of structure within the herbivore trophic level

To test whether structural stability of community persistence can provide a biologically sound description of structure within the herbivore trophic level, we compared the extent to which the structural changes generated by wild self-sustained plants are similar to the changes generated by non-self-sustained ornamental plants. Because our measure of structural stability is linked to community persistence, we hypothesized that ornamental plants, which are non-self-sustained, should play a different role than persistent plants when building the structure within the herbivore trophic level. To measure this, we divided our data into a subset of wild self-sustained plants and a subset of ornamental plants. Then, we used each subset to investigate the corresponding structural changes across time. We calculated the level of similarity in structural changes by the partial Pearson correlation between the two temporal sequences controlling for time t in order to avoid spurious correlations (Iler et al., 2017).

Additionally, to validate that structural changes are not just a byproduct of community size, we naively randomized the observed plant arrivals but preserved the observed number of plants per year. Then, we calculated the corresponding distribution of

correlations between structural stability and time $r(t,\omega(\boldsymbol{A_t}))$. If structural changes are not an artifact of the number of species and interactions observed in the data, we expected this distribution to be different from the observed correlation. Finally, to illustrate the added value of our measure of structural stability, we repeated the entire analysis using standard global network descriptors (Clauset et al., 2004; Pons and Latapy, 2005; Almeida-Neto et al., 2008). Because it has been shown that these network descriptors fail to capture important differences between structures (Saavedra et al., 2017*a*) and null models cannot be used across different data sets to solve this problem (Song et al., 2017), we expected to see no significant differences in time series between wild self-sustained and ornamental plants with these other structural measures.

Testing simple assembly rules acting on the plant trophic level

To investigate the association between the order of assembly in the plant trophic level and structural changes within the herbivore trophic level, we compared the observed correlation between structural stability and time $r(t,\omega(\boldsymbol{A_t}))$ against the statistical ensemble of correlations generated by two random orders of plant arrivals taking into account family-level information. Note that we classified plants according to groups at the family-level as they have been found to be among the major determinants of herbivore associations of plants (Ehrlich and Raven, 1964; Fox, 1987; Pearse and Altermatt, 2013*b*). We have 54 different families in our data. The first random assembly allows the arrival of any plant at any time, but preserves the order at which families arrive. The second random assembly also allows the arrival of any plant at any time, but preserves the order within families. Note that the number of plants per year is also preserved in both randomizations. Thus, the first and second random assemblies impose hierarchical constraints on the arrival of species from different functional groups (distantly-related species) and on the arrivals of species within functional groups (closely-related species), respectively. These assembly mechanisms have been broadly investigated (Fox, 1987; Fukami et al., 2005), and their rationale is based on the observations that diet selection can facilitate the arrival of species from different functional groups until each group is represented before the cycle repeats.

For example, let us classify six plant species i into two different families, denoted as X_i and Y_i and $i = 1, 2, 3$. Let us now suppose that the order of arrival is $X_1Y_1X_2X_3Y_2Y_3$.

This generates structural changes within the herbivore trophic level defined by an ordered vector $[\omega(X_1), \omega(X_1Y_1), \omega(X_1Y_1X_2), \omega(X_1Y_1X_2X_3), \omega(X_1Y_1X_2X_3Y_2), \omega(X_1Y_1X_2X_3Y_2Y_3)]$, which is then correlated to a time vector $[t_1, t_2, t_3, t_4, t_5, t_6]$. Then, testing the constraints introduced by preserving the order of families can lead us to a randomization such as $X_2Y_3X_1X_3Y_1Y_2$, where the order of arrival of species i within families X and Y is randomized, but the order at which families arrive is preserved. Similarly, testing the constraints introduced by preserving the order of plant arrivals within families can lead us to a random sequence such as $Y_1Y_2X_1X_2X_3Y_3$, where in this case the randomization occurs across X and Y, but the order of species i within its own family remains the same (see Fig. 1 for a graphical example).

Because each random assembly generates a distribution of correlations between structural stability and time, we performed a standard likelihood test (Legendre and Legendre, 2012) to quantify the extent to which each random mechanism can explain the observed correlation. The distribution of correlations generated by each random assembly is taken as a normal distribution with mean and variance calculated from the simulations. Thus, the likelihood that each random assembly generates the observed correlation is calculated as the probability in the corresponding distribution of the hypothesis. Then, we calculated the ratio between the likelihoods of the first and second random assemblies. Note that ratios greater than 1 indicate that the order of distantly-related plant species can explain better the observed structural changes within the herbivore trophic level, whereas ratios lower than 1 indicate that the observed structural changes are better explained by the order of closely-related plant species.

Results

Structural changes within the herbivore trophic level

We found that the observed order of plant arrivals generated a non-trivial increase of structural stability of community persistence within the herbivore trophic level across time. Figure 2 shows that the estimated structural stability given by the inferred competition matrices $\omega(\boldsymbol{A_t})$ generally increased across the observation period. Specifically, we found a positive trend characterized by a correlation between structural

stability and time of $r(t,\omega(\boldsymbol{A_t})) = 0.89$ ($[0.83, 0.92]$ 95% confidence interval). This positive trend is robust to both potential sampling errors (see Fig. S2) and the split of the time series into two different periods (before and after 1500 AD) (see Fig. S3).

We also found, as expected, that this positive trend is characteristic of wild self-sustained plants, but not of ornamental plants. Figure 3 shows that while structural changes generated by the subset of wild self-sustained plants have a correlation with the overall trend (see Fig. 2) of 0.88 ($[0.81, 0.92]$ 95% confidence interval), structural changes generated by the subset of ornamental plants have a low correlation of 0.27 ($[0.07, 0.45]$ 95% confidence interval). Importantly, the correlation between the structural changes generated by wild self-sustained and ornamental plants is 0.04 (statistically non-significant), confirming that our measure of structural stability can detect differences in the effect of these two groups of plants on the herbivore trophic level. In contrast, standard network metrics fail to detect differences between these two time series (see Figs. S4-S7).

Importantly, we found that the positive trend observed for structural stability within the herbivore trophic level is not an artifact of community size and it is highly unlikely to be reproduced by randomly (naively) shuffling plant arrivals (see Fig. 4). In fact, the expected correlation between structural stability and time generated by random plant arrivals is negative (-0.39), revealing that an increase in structural stability within the herbivore trophic level over the entire observation period is highly unlike to be generated by a random assembly of the plant trophic level.

The importance of the order of assembly within plant families

Finally, we found that as long as the order of arrival of closely-related plant species is preserved, all the other plant arrivals can happen randomly and still herbivore species would have been constrained to the same observed structural changes. Figure 4 shows that by randomizing plant arrivals while preserving the order of families, the generated distribution of correlations $r(t,\omega(\boldsymbol{A_t}))$ is statistically indistinguishable from zero. In contrast, by randomizing plant arrivals while preserving the order within families, all correlations are highly positive as it was observed. In fact, the likelihood ratio of generating the observed correlation between the first and second random assembly

mechanisms is 0.1, confirming that only the order of introduction of closely-related plant species can explain the observed structural changes within the herbivore trophic level. These results remain qualitatively robust even if we separate the time series into two different periods (see Figs. S8-S9).

Discussion

Earlier work has used paleoecological data to show the long-term impact of the order of species arrivals on community composition (presence and absence of species) within trophic levels (Duncan and Forsyth, 2006; Mergeay et al., 2011). Within this long-term context, our work provides a new direction toward understanding the impact of the assembly order at basal trophic levels on the structure of consumer trophic levels. We have investigated this structure through the lens of structural stability of community persistence, i.e., the extent to which the interaction matrix modulates the conditions (parameter values) compatible with persistent herbivore populations. In our study, we have found that the herbivore trophic level generally increased its level of structural stability across time (see Fig. 2). We have found that the order of arrival of closely-related (but not of distantly-related) plant species constrained the structural changes within the herbivore trophic level as they were observed (see Fig. 4). This implies that if we were to rewind the tape of life and replay it in this community, we should pay particular attention to the factors shaping the order at which plants arrive within their own family. Specifically, the existence of alternative structures within the herbivore trophic level may depend on how early-arriving plant species affect the arrival of closely-related plant species more than they affect the arrival of distantly-related plant species.

Our findings above suggest that there are two important ecological mechanisms operating at two different trophic levels. The first mechanism operates at the basal (plant) trophic level and it may be characterized by niche preemption—a priority effect acting within functional groups or within similarly competitive species (Fukami, 2015). That is, the importance of the order of arrival of closely-related plants indicates the effect of a strong preemption (hierarchical) mechanism acting within functional groups of plants. This preemption mechanism within families can arrive during successional development as a

consequence of already highly-exploited niches (Odum, 1969). Alternatively, this ordering may be the outcome of a nonrandom presence of propagule pressure in which generalist host-plants tend to arrive earlier than specialists (Pearse and Altermatt, 2013*b*). Note that we did not explicitly model competition among plants. Instead, we modeled the process of diversification of host-plants through the randomization of the order of plant arrivals. This assumes that the assembly process of the plant trophic level converges to the same community composition at the end of the observation period.

The second mechanism operates at the consumer (herbivore) trophic level and it may be the result of the dynamics acting at the lower (plant) trophic level. That is, our data revealed a positive trend of structural stability of community persistence within the herbivore trophic level over 2000 years (see Fig. 2). Recall that the higher the level of structural stability, the larger the tolerance of a community to random environmental changes. Because our definition of structural stability is inversely related to the overall level of resource overlap (Rohr et al., 2016; Cenci et al., 2018), the observed non-trivial positive trend also indicates a non-trivial increase in resource partitioning. This implies that the herbivore community favored structures with high overlap of host-plants during the early assembly stages, but this overlap dilutes as the community matured. Importantly, this trend can be attributed to the observed order of plant arrivals within families (see Fig. 4). Without preserving any order of arrivals, our simulations have revealed that the structural stability of the community would have decreased over time. Similarly, by only preserving the order of arrivals across families (but not within), on average there would have been no trend whatsoever. Therefore, an observed increase of structural stability in the herbivore community for over 2000 years may indicate potential non-adaptive dynamics as the result of the particular constraints imposed by the plant trophic level (acting as environmental conditions) (Tregonning and Roberts, 1979; Borrelli et al., 2015; Saavedra et al., 2016*a*; Song et al., 2017).

Focusing on the observed trend of structural stability of community persistence (Figs. 2 and S3), it is worth noting that the breakpoint around the year 1500 A.D. may have various ecological consequences, such as an increase in the number of non-native plants, as well as a the arrival of plants from a previously completely disconnected biogeographic area, namely the Americas (see Fig. S1). Unfortunately, we do not have knowledge on

systematic ecological differences between these plants, but clearly they represent some previously separated pools of species that may have different effects on the structural stability of the system. Yet, our randomization results have indicated that no single species is responsible for the observed trend of structural changes within the herbivore trophic level. This has been confirmed by noticing that a naive random assembly cannot generate a positive trend of structural stability across time (see Fig. 4). Thus, the impact of a newly-introduced species on the structure of a community is time dependent, especially an order-dependent process within functional groups. This can be the reason why many times invasive species are found without significant impact on the structure of a community when analyzed using non-temporal data (Stouffer et al., 2014). Overall, our results imply that structural changes within consumer trophic levels may be explained and anticipated by assembly rules within functional groups operating on basal trophic levels and the environmental pressures acting on the focal trophic level. Thus, future work should focus on disentangling the impact of these two forces on the structure and dynamics of trophic levels.

References

Alberch, P. 1989. The logic of monsters: Evidence for internal constraint in development and evolution. Geobios 22:21–57.

Almeida-Neto, M., Guimarães, P., Guimarães Jr, P. R., Loyola, R. D., and Urlich, W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239.

Altermatt, F. and Pearse, I. S. 2011. Similarity and specialization of the larval versus adult diet of european butterflies and moths. The American Naturalist 178:372–382.

Borrelli, J. J., Allesina, S., Amarasekare, P., Arditi, R., Chase, I., Damuth, J., Holt, R. D., Logofet, D. O., Novak, M., Rohr, R. P., Rossberg, A. G., Spencer, M., Tran, J. K., and Ginzburg, L. R. 2015. Selection on stability across ecological scales. Trends in Ecology and Evolution 30:417–425.

Brändle, M., Kühn, I., Klotz, S., Belle, C., and Brandl, R. 2008. Species richness of herbivores on exotic host plants increases with time since introduction of the host. Diversity Distrib. 14:905–912.

Case, T. J., 2000. An Illustrated Guide to Theoretical Ecology. Oxford Univ. Press, Oxford.

Cenci, S., Montero-Castaño, A., and Saavedra, S. 2018. Estimating the effect of the reorganization of interactions on the adaptability of species to changing environments. J. of Theor. Bio. 437:115–125.

Cenci, S. and Saavedra, S. 2018. Structural stability of nonlinear population dynamics. Phys. Rev. E 97:012401.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia 136:489–498.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. Science 328:1388–1391.

Clauset, A., Newman, M. E., and Moore, C. 2004. Finding community structure in very large networks. Physical Review E 70:066111.

385 Diamond, J., 1975. Assembly of species communities. Pages 342–444 *in* M. L. Cody and
386 J. M. Diamond, eds. Ecology and evolution of communities. Harvard Univ. Press,
387 Cambridge.

388 Dormann, C. F., Fründ, J., and Schaefer, H. M. 2017. Identifying causes of patterns in
389 ecological networks: Opportunities and limitations. Annual Review of Ecology,
390 Evolution, and Systematics 48:559–584.

391 Drake, J. A. 1991. Community assembly mechanics and the structure of an experimental
392 species ensemble. Am. Nat. 137:1–26.

393 Duncan, R. P. and Forsyth, D. M., 2006. Competition and the assembly of introduced
394 bird communities, Pages 415–431. Springer, Dordrecht.

395 Ebert, G., 1991-2005. Die Schmetterlinge Baden-Württembergs. Vol. I–X. Ulmer,
396 Stuttgart.

397 Ehrlich, P. R. and Raven, P. H. 1964. Butterflies and plants: A study in coevolution.
398 Evolution 18:586–608.

399 Faillace, C. A. and Morin, P. J. 2016. Evolution alters the consequences of invasions in
400 experimental communities. Nature Ecology and Evolution 1:0013.

401 Fox, B. J. 1987. Species assembly and the evolution of community structure. Evol. Ecol.
402 1:201–213.

403 Fukami, T. 2015. Historical contingency in community assembly: integrating niches,
404 species pools, and priority effects. Annual Review of Ecology, Evolution, and
405 Systematics 46:1–23.

406 Fukami, T., Bezemer, T. M., Mortimer, S. R., and der Putten, W. H. V. 2005. Species
407 divergence and trait convergence in experimental plant community assembly. Ecology
408 Letters 8:1283–1290.

409 Fukami, T. and Morin, P. J. 2003. Productivity–biodiversity relationships depend on the
410 history of community assembly. Nature 424:423–426.

411 Godoy, O., Bartomeus, I., Rohr, R. P., and Saavedra, S. 2018. Towards the integration of
412 niche and network theories. Trends in Ecology and Evolution 33:287–300.

Gomes, S. I. F., Merckx, V. S. F. T., and Saavedra, S. 2017. Fungal-host diversity among mycoheterotrophic plants increases proportionally to their fungal-host overlap. Ecology and Evolution 7:3623–3630.

Gould, S. J., 1989. Wonderful Life. W. W. Norton & Co, New York.

Gripenberg, S., Morri en, E., Cudmore, A., Salminen, J., and Roslin, T. 2007. Resource selection by female moths in a heterogeneous environment: what is a poor girl to do? J. of Anim. Ecology 76:854–885.

Hairston, N. G., Smith, F. E., and Slobodkin, L. B. 1960. Community structure, population control, and competition. The American Naturalist 94:421–425.

Iler, A. M., Inouye, D. W., Schmidt, N. M., and Hoye, T. T. 2017. Detrending phenological time series improves climatephenology analyses and reveals evidence of plasticity. Ecology 98:647–655.

Jacomet, S. and Brombacher, C. 2009. Geschichte der flora in der regio basiliensis seit 7500 jahren: Ergebnisse von untersuchungen pflanzlicher makroreste aus archäologischen ausgrabungen. Mitteilungen der Naturforschenden Gesellschaften beider Basel 11:27–106.

Klotz, S., Kühn, I., Durka, W., and Briemle, G., 2002. BIOLFLOR: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland, volume 38. Bundesamt für naturschutz Bonn.

Legendre, P. and Legendre, L., 2012. Numerical Ecology, 3rd edition. Elsevier, Amsterdam.

Leopold, D. R., Wilkie, J. P., Dickie, I. A., Allen, R. B., Buchanan, P. K., and Fukami, T. 2017. Priority effects are interactively regulated by top-down and bottom-up forces: evidence from wood decomposer communities. Ecology Letters 20:1054–1063.

Logofet, D. O., 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press, Moscow.

MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

Mergeay, J. L., Meester, L. D., Eggermont, H., and Verschuren, D. 2011. Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. Ecology 92:2267–2275.

Morin, P. J., 2011. Community ecology (second edition). John Wiley & Sons, London.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Olito, C. and Fukami, T. 2009. Long-term effects of predator arrival timing on prey community succession. Am. Nat. 173:354–362.

Pearse, I. S. and Altermatt, F. 2013*a*. Extinction cascades partially estimate herbivore losses in a complete Lepidoptera–plant food web. Ecology 94:1785–1794.

Pearse, I. S. and Altermatt, F. 2013*b*. Predicting novel trophic interactions in a non-native world. Ecology Letters 16:1088–1094.

Pearse, I. S. and Altermatt, F. 2015. Out-of-sample predictions from plant–insect food webs: robustness to missing and erroneous trophic interaction records. Ecological Applications 25:1953–1961.

Pons, P. and Latapy, M., 2005. Computing communities in large networks using random walks. *in* International symposium on computer and information sciences, Pages 284–293. Springer.

Price, J. E. and Morin, P. J. 2004. Colonization history determines alternate community states in a food web of intraguild predators. Ecology 85:1017–1028.

Ribando, M. J. 2006. Measuring solid angles beyond dimension three. Discrete & Computational Geometry 36:479–487.

Rohr, R. P., Saavedra, S., Peralta, G., Frost, C. M., Bersier, L.-F., Bascompte, J., and Tylianakis, J. M. 2016. Persist or produce: a community trade-off tuned by species evenness. Am. Nat. 188:411–422.

Saavedra, S., Cenci, S., del Val, E., Boege, K., and Rohr, R. P. 2017*a*. Reorganization of interaction networks modulates the persistence of species in late successional stages. J. of Animal Ecology 86:1136–1146.

Saavedra, S., Rohr, R. P., Bascompte, J., Godoy, O., Kraft, N. J. B., and Levine, J. M. 2017*b*. A structural approach for understanding multispecies coexistence. Ecol. Monogr. 87:470–486.

Saavedra, S., Rohr, R. P., Fortuna, M. A., , Selva, N., and Bascompte, J. 2016*a*. Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence. Ecology 97:865–873.

Saavedra, S., Rohr, R. P., Gilarranz, L. J., and Bascompte, J. 2014. How structurally stable are global socioeconomic systems? J. R. Soc. Interface 11:20140693.

Saavedra, S., Rohr, R. P., Olesen, J. M., and Bascompte, J. 2016*b*. Nested species interactions promote feasibility over stability during the assembly of a pollinator community. Ecology and Evolution 6:997–1007.

Sebald, O., Seybold, S., Philippi, G., and Wörz, A., 1993-1998. Die Farn- und Blütenpflanzen Baden-Württembergs. Ulmer, Stuttgart.

Song, C., Rohr, R. P., and Saavedra, S. 2017. Why are some plant–pollinator networks more nested than others? Journal of Animal Ecology 86:1417–1424.

Stouffer, D. B., Cirtwill, A. R., and Bascompte, J. 2014. How exotic plants integrate into pollination networks. Journal of Ecology 102:1442–1450.

Tack, A., Ovaskainen, O., Harrison, P. H., and Roslin, T. 2009. Competition as a structuring force in leaf miner communities. Oikos 118:809–818.

Thom, R., 1972. Stabilité structurelle et morphogenèse. InterÉditions, Paris.

Thompson, D. W., 1917. On Growth and Form. Cambridge Univ. Press, Cambridge.

Tregonning, K. and Roberts, A. 1979. Complex systems which evolve towards homeostasis. Nature 281:563–564.

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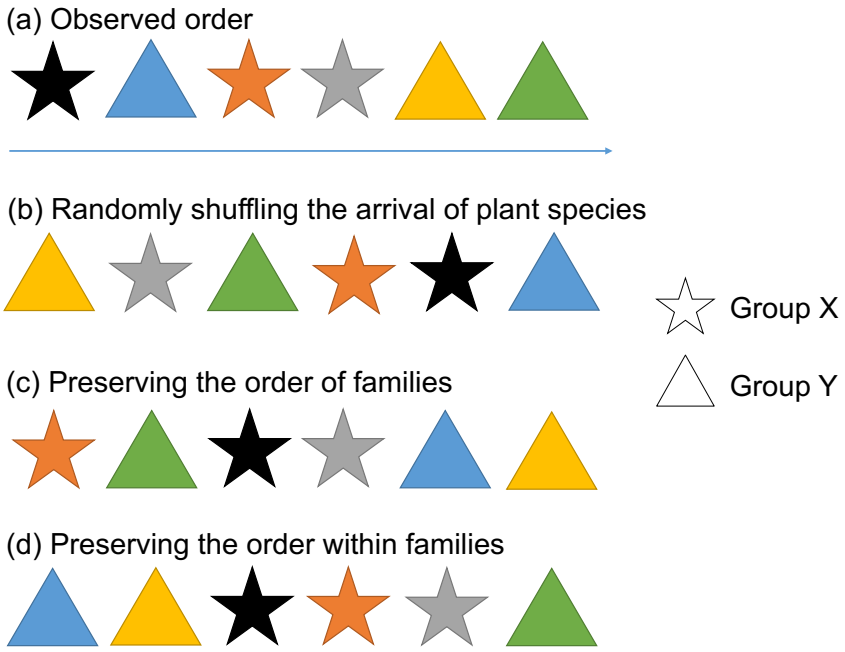

Figure 1: **Graphical example of random assembly mechanisms for plant arrivals**. We considered a hypothetical sequence of plant arrivals with two families (functional groups) X (star) and Y (triangle), and each family contains three species labeled $1, 2, 3$, respectively. Panel (**a**) shows the hypothesized sequence $X_1Y_1X_2X_3Y_2Y_3$, showing that X_1 arrives before Y_1, and Y_1 arrives before X_2, and so on. Panel (**b**) shows an example of a naive randomization of the observed arrival sequence by randomly shuffling the order of plant arrivals. Panel (**c**) shows an example of a randomization of the observed arrival sequence while preserving the order of families. Panel (**d**) shows a randomization of the observed arrival sequence while preserving the order within families.

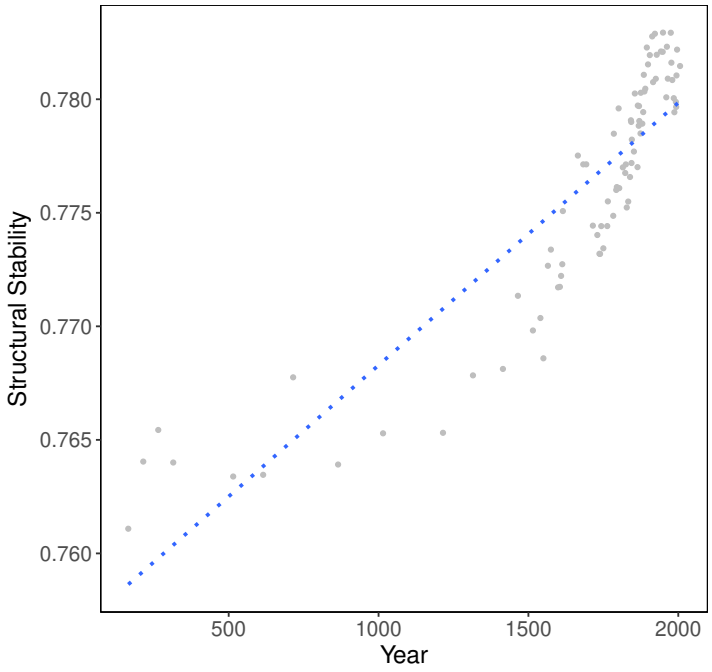

Figure 2: **Structural changes within the herbivore trophic level across time.** We use the structural stability of community persistence as a measure of structure within the herbivore trophic level. Each point corresponds to the estimated level of structural stability for the inferred competition matrix at a given year $\omega(\boldsymbol{A_t})$. This figure shows that the estimated structural stability generally increased over time (Pearson correlation of 0.89 with 95% confidence $[0.83, 0.92]$). The linear-regression line is depicted only to show the trend.

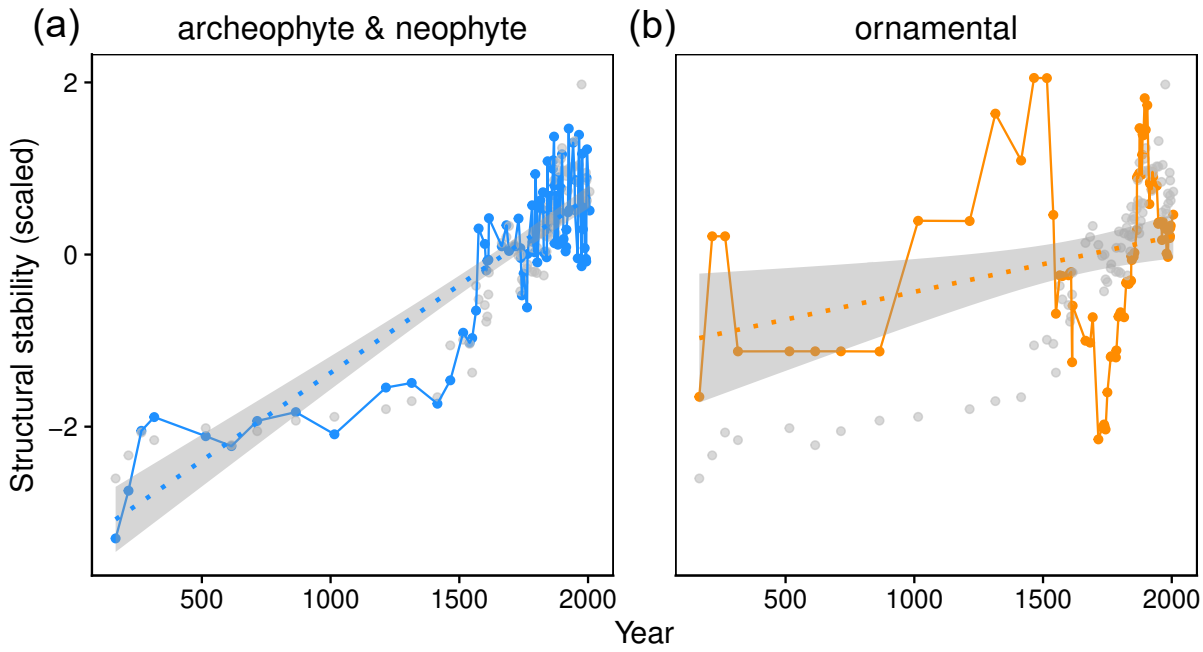

Figure 3: **Validating structural stability as a measure of structure within herbivore trophic level.** Panels **(a)** and **(b)** show (solid lines) the structural changes (measured by the estimated level of structural stability of community persistence) generated by the inferred competition matrices from the subsets of wild self-sustained and ornamental plants, respectively. The correlation in Panel **(a)** is 0.88 ($[0.81, 0.92]$ 95% confidence interval), and the correlation in Panel **(b)** is 0.27 ($[0.07, 0.45]$ 95% confidence interval). The values of structural stability are scaled for visualization purposes. The gray points in the background show the pattern generated by the two subsets together (identical to Fig. 2). The linear-regression lines are depicted with shaded 95% confidence intervals.

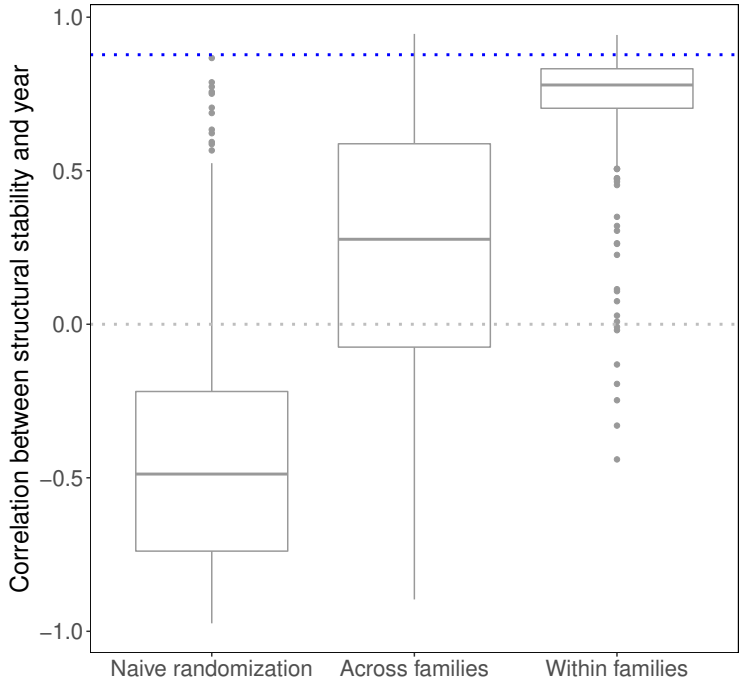

Figure 4: **Impact of the plant assembly order on structural changes within the herbivore trophic level**. The blue dotted line shows the observed positive correlation of 0.89 between structural stability of community persistence and year $r(t,\omega(\boldsymbol{A_t}))$. The boxplots correspond to the distribution of correlations generated by three random plant assembly mechanisms: randomly shuffling plant arrivals (left boxplot), randomly shuffling plant arrivals while preserving the order at which families arrive (middle boxplot), and randomly shuffling plant arrivals while preserving the order within families (right boxplot). The figure shows that preserving the order of assembly of closely-related species (right boxplot) is more likely to generate high positive correlations similar to the observed case. Boxplots depict the inter-quartile range and the solid line corresponds to the median value. The gray dotted line centered at zero (y-axis) is just intended to serve as a reference guide.

Supporting Information for Structural changes within trophic levels are constrained by within-family assembly rules at lower trophic levels

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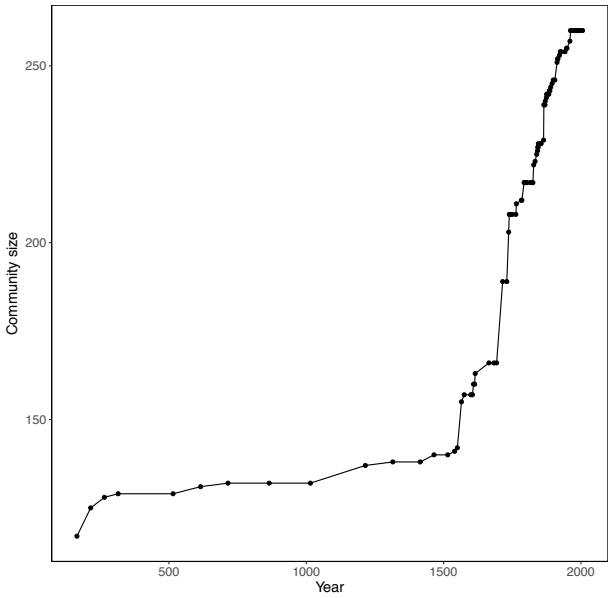

Figure S1: [Supplementary Figure] **Number of species at the herbivore trophic level across time**. Each point corresponds to the number of herbivore species (i.e., community size) at a give point in time across our observational period.

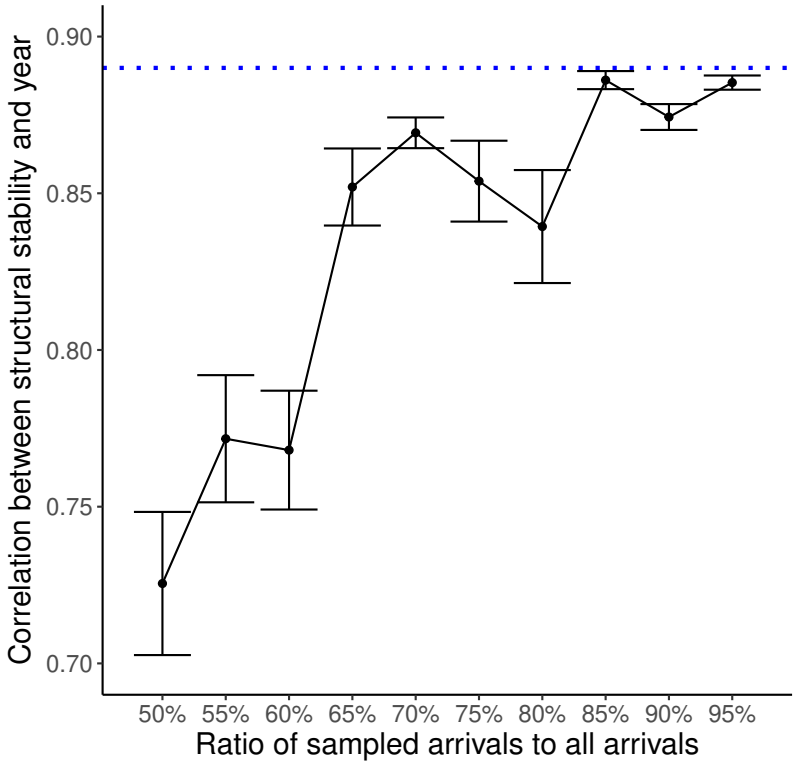

Figure S2: [Supplementary Figure] **Sensitivity analysis to sampling error**. To perform a sensitivity analysis of the effect of sampling error on the observed correlation between structural stability and time, we systematically sampled different fractions of randomly chosen plants (mimicking the process that some plants might not be documented due to sampling error). Each point corresponds to the mean correlation of 50 randomizations with the standard error depicted as error bars. The red line corresponds to the Pearson correlation of structural stability and year in the observed data. Note that even for a lost of 50% of the data, the correlation continues to be highly positive.

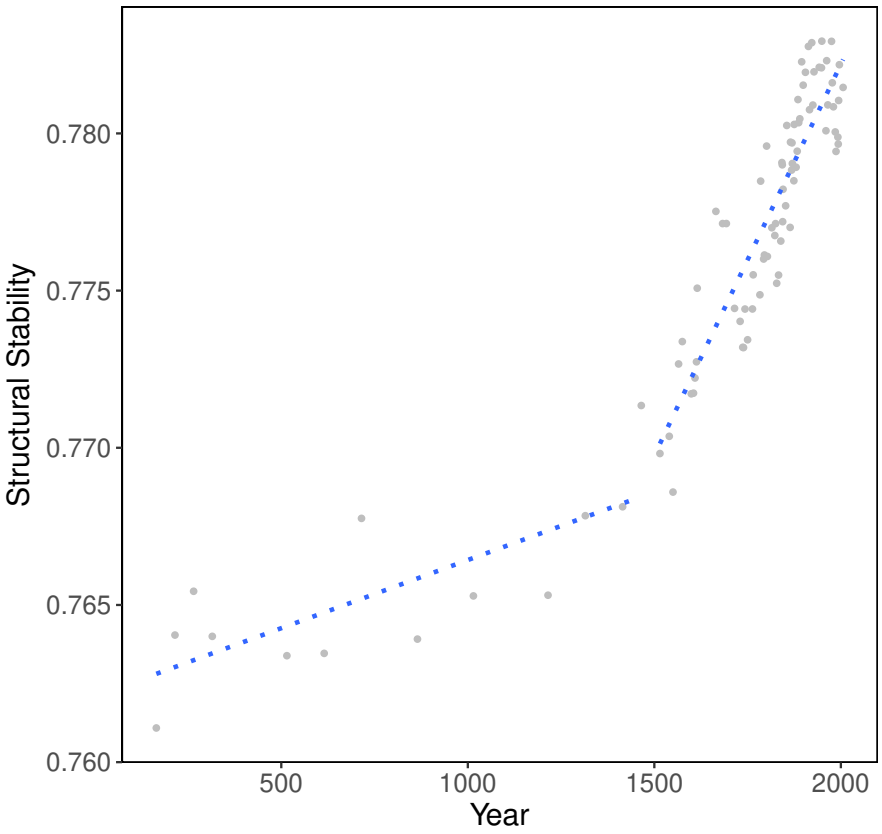

Figure S3: [Supplementary Figure] **Sensitivity analysis to time series division.** Identical to Figure 2 in the main text except that the correlations are calculated separately for the periods before and after 1500 AD. The correlation before 1500 AD is 0.76 ([0.37, 0.93] 95% confidence interval), and the correlation after 1500 AD is 0.89 ([0.83, 0.93] 95% confidence interval). The (scaled) estimated linear effect of year on structural stability before 1500 AD is 0.33 (0.08 standard error), and after 1500 AD is 1.91 (0.11 standard error).

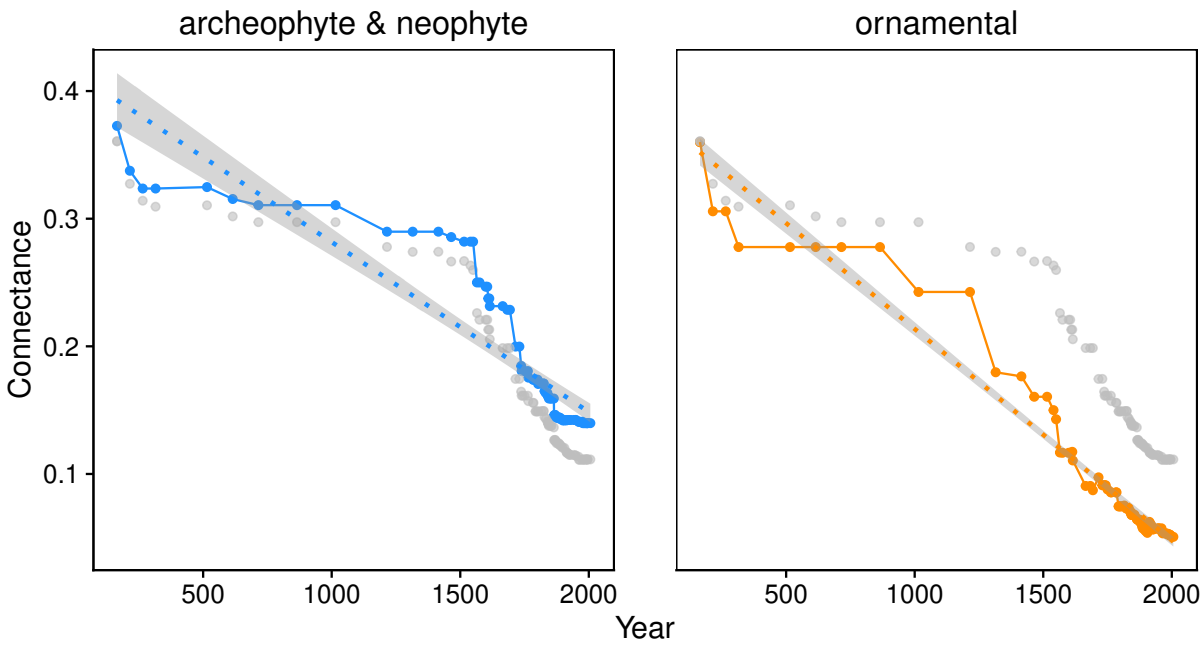

Figure S4: [Supplementary Figure] **Using standard network metrics**. Similar to Figure 3 in the main text. Here the colored symbols represent changes of network connectance (defined as the observed number of direct interactions over the maximum possible number) calculated over the inferred competition networks from the subsets of wild self-sustained and ornamental plants, respectively. The correlation in Panel **(a)** is -0.90 ($[-0.94, -0.86]$ 95% confidence interval), and the correlation in Panel **(b)** is 0.27 ($[-0.99, -0.97]$ 95% confidence interval). The partial correlation between the two panels is 0.62, revealing no difference in connectance changes between the two time series. The gray points in the background show the pattern generated by the two subsets together. The linear-regression lines are depicted with shaded 95% confidence intervals.

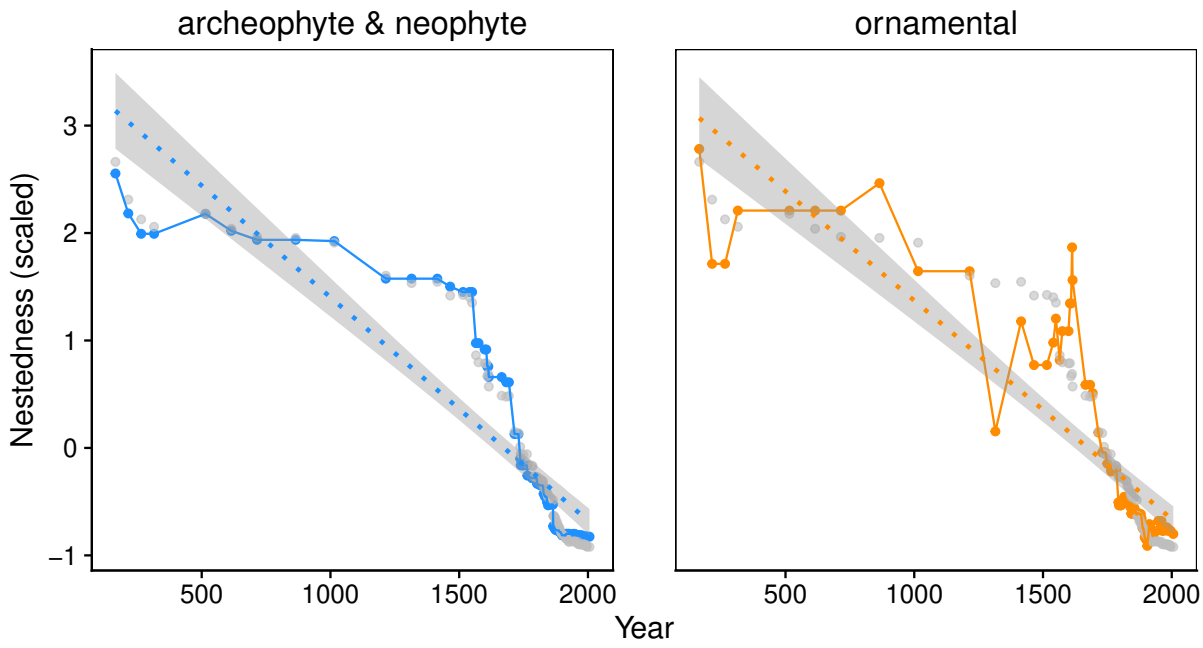

Figure S5: [Supplementary Figure] **Using standard network metrics**. Similar to Figure 3 in the main text. Here the colored symbols represent changes in nestedness of the herbivore-plant binary interaction matrix (measured as NODF (Almeida-Neto et al., 2008)) generated by the subsets of wild self-sustained and ornamental plants, respectively. The values of nestedness are scaled for visualization purposes. The correlation in Panel **(a)** is -0.89 ($[-0.93, -0.84]$ 95% confidence interval), and the correlation in Panel **(b)** is -0.87 ($[-0.91, -0.81]$ 95% confidence interval). The partial correlation between the two panels is 0.81, revealing no difference in nestedness changes between the two time series. The gray points in the background show the pattern generated by the two subsets together. The linear-regression lines are depicted with shaded 95% confidence intervals.

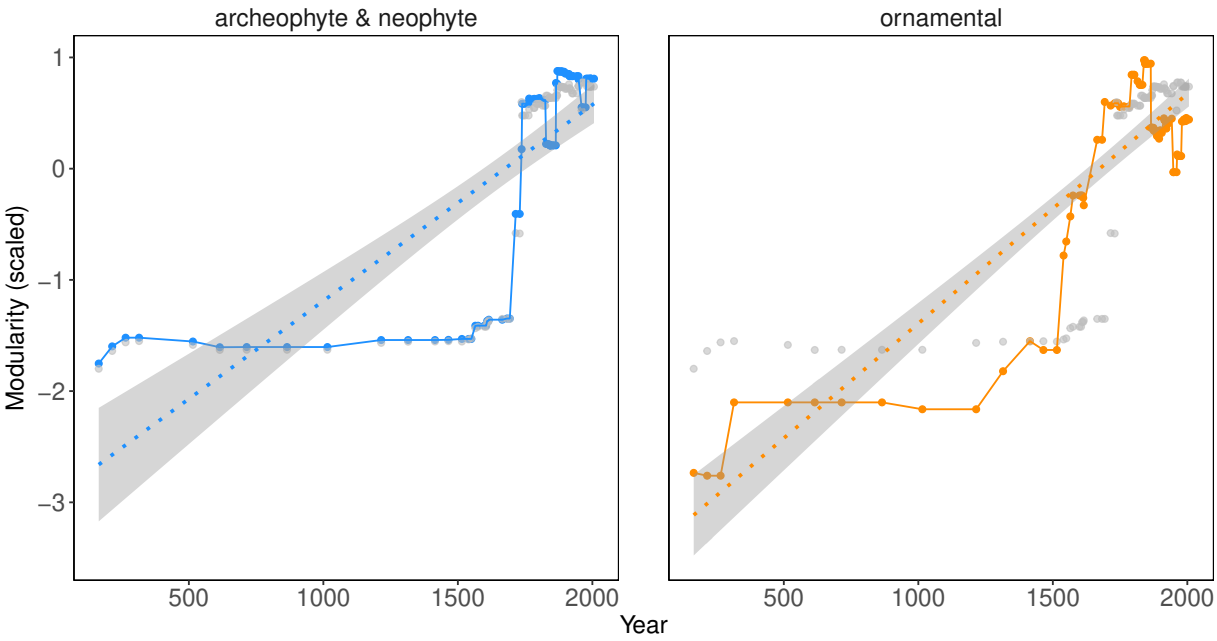

Figure S6: [Supplementary Figure] **Using standard network metrics**. Similar to Figure 3 in the main text. Here the colored symbols represent changes in modularity of the inferred competition matrices from the subsets of wild self-sustained and ornamental plants (measured following Refs. (Clauset et al., 2004; Pons and Latapy, 2005)). The values of modularity are scaled for visualization purposes. The correlation in Panel **(a)** is 0.76 ($[0.65, 0.83]$ 95% confidence interval) and the correlation in Panel **(b)** is 0.88 ($[0.83, 0.92]$ 95% confidence interval). The partial correlation between the two panels is 0.32, revealing no difference in modularity changes between the two time series. The gray points in the background show the pattern generated by the two subsets together. The linear-regression lines are depicted with shaded 95% confidence intervals.

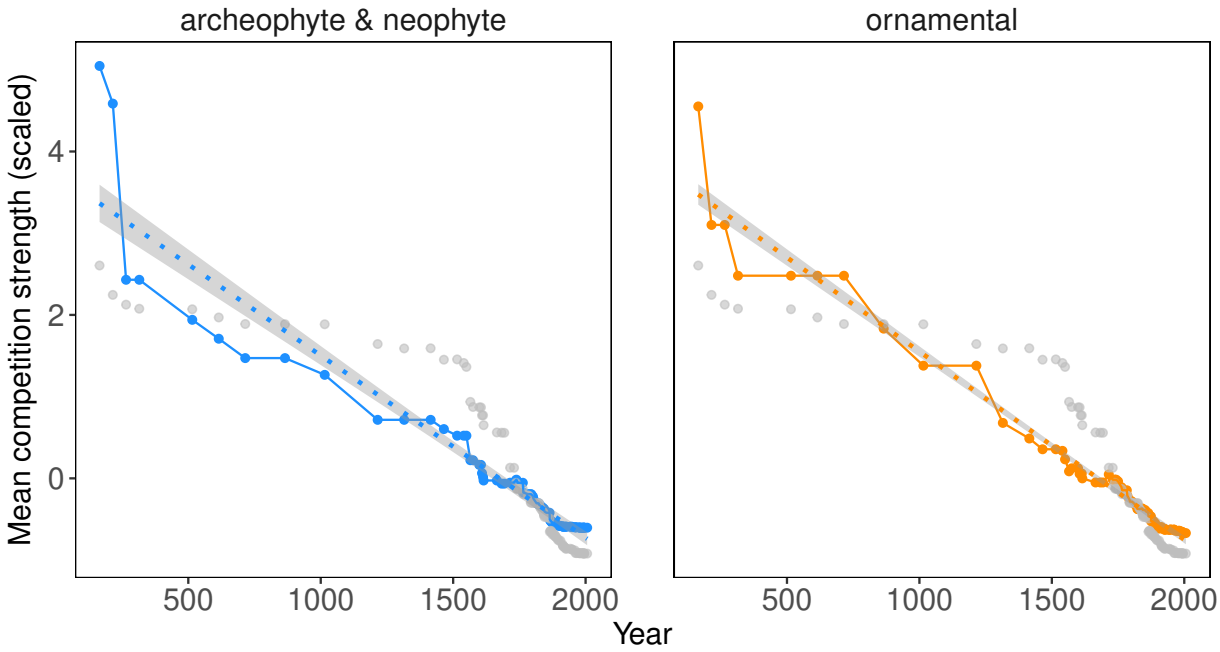

Figure S7: [Supplementary Figure] **Using standard network metrics**. Similar to Figure 3 in the main text. Here the colored symbols represent changes in mean interspecific competition strength generated by the inferred competition matrices from the subsets of wild non-native and ornamental plants, respectively. The values of mean competition strength are scaled for visualization purposes. The correlation in Panel **(a)** is -0.95 ($[-0.97, -.94]$ 95% confidence interval), and the correlation in Panel **(b)** is -0.99 ($[-0.99, -0.98]$ 95% confidence interval). The partial correlation between the two panels is 0.5, revealing no difference in competition-strength changes between the two time series. The gray points in the background show the pattern generated by the two subsets together. The linear-regression lines are depicted with shaded 95% confidence intervals.

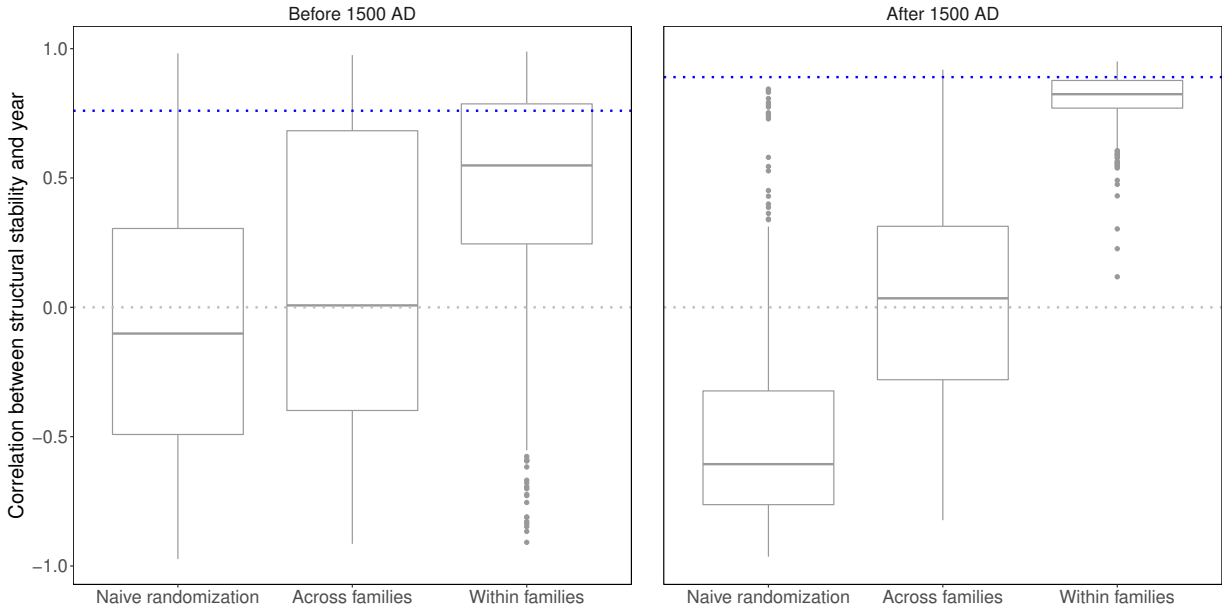

Figure S8: [Supplementary Figure] **Split sample test about the positive trend of structural stability**. Similar to Figure 4 in the main text except that the analysis is performed for the two periods before and after 1500 AD (see Figure S3). The qualitative result remains the same as in Figure 4.

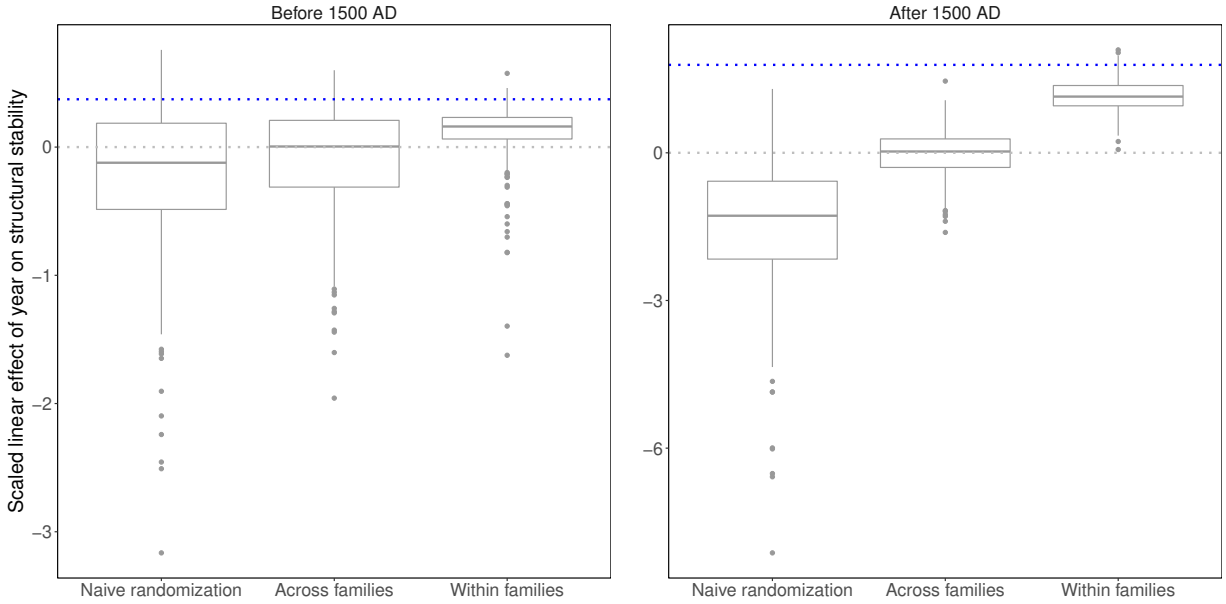

Figure S9: [Supplementary Figure] **Split sample test about the positive trend of structural stability**. Similar to Figure 4 in the main text except that the analysis is performed for the two periods before and after 1500 AD (see Figure S3), and the y-axis corresponds to the estimated linear effect of year on structural stability. The qualitative result remains the same as in Figure 4.